

*INTERTRIAL-INTERVAL EFFECTS ON SENSITIVITY (A')  
AND RESPONSE BIAS (B') IN A TEMPORAL  
DISCRIMINATION BY RATS*

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Killeen and Fetterman's (1988) behavioral theory of animal timing predicts that decreases in the rate of reinforcement should produce decreases in the sensitivity (A') of temporal discriminations and a decrease in miss and correct rejection rates (decrease in bias toward "long" responses). Eight rats were trained on a 10- versus 0.1-s temporal discrimination with an intertrial interval of 5 s and were subsequently tested on probe days on the same discrimination with intertrial intervals of 1, 2.5, 5, 10, or 20 s. The rate of reinforcement declined for all animals as intertrial interval increased. Although sensitivity (A') decreased with increasing intertrial interval, all rats showed an increase in bias to make long responses.

*Key words:* time discrimination, intertrial interval, signal detection, response bias, lever pressing, rats

Killeen and Fetterman (1988) have proposed a theory of animal timing that formalizes the notion that behavior mediates temporal control. In their theory, reinforcing stimuli "engender" adjunctive behavior that can become conditioned to serve as discriminative stimuli in timing experiments. Different classes of adjunctive behavior (behavioral states) occur between reinforcing stimuli, and transitions between these classes are produced by pulses from an "internal clock." Thus, "in timing experiments, if an animal is interrupted while in some state and asked to respond *short* or *long*, it will make whichever response has been most often associated with reinforcement in the context of behaviors associated with that state" (Killeen & Fetterman, 1988, p. 274). Transitions between behavioral states are modeled by a Poisson process with a rate constant  $\tau$ ,

which is inversely proportional to the rate of reinforcement:

$$p[N(t) = n] = [(t/\tau)^n e^{-t/\tau}] / n!, \quad (1)$$

where  $p[N(t) = n]$  is the probability that the number of pulses received by time  $t$  equals  $n$ , and  $\tau$  is the average time between pulses. Thus the rate of reinforcement in an experiment should affect timing performance. For instance, Killeen and Fetterman predict that "transient shifts in the psychometric function should be visible when the rate of reinforcement is altered," and that "the standard deviation should increase with increases in  $\tau$ , and the resulting decrease in accuracy should be durable" (p. 281). They specifically predict that a decrease in reinforcement rate should increase  $\tau$  and produce a decrease in the probability of long responses (p. 282).

Killeen and Fetterman (1988) have shown that Equation 1 can be simplified to an exponential decay function (p. 281) for certain stimulus conditions. For instance, if a brief duration such as 0.1 s is used as a discriminative stimulus, they assume that *no* clock pulses will have been registered, so that  $n = 0$  in Equation 1. The probability of being in that state, then, is

$$p[N(t) = 0] = [(t/\tau)^0 e^{-t/\tau}] / 0!, \quad (2)$$

or

$$p[N(t) = 0] = e^{-t/\tau}, \quad (3)$$

The research described in this report was conducted in compliance with the Animal Welfare Act and other federal statutes and regulations relating to animals and experiments involving animals and adheres to the principles stated in the *Guide for the Care and Use of Laboratory Animals*, NIH publication 85-23. The views of the author(s) do not purport to reflect the position of the Department of the Army or the Department of Defense (para 4-3, AR 360-5). The authors acknowledge the helpful criticism and comments provided by Michael Davison and Peter Killeen in the revision of this manuscript. Special thanks are due to Peter Killeen for providing a fit of the cumulative normal version of behavioral timing theory for the data. Correspondence should be directed to Thomas G. Raslear, Department of Microwave Research, WRAIR, Washington, D.C. 20307-5100.

		RESPONSE	
		"SHORT"	"LONG"
SIGNAL	SHORT	HIT $e^{-s/\tau}$	MISS $1 - e^{-s/\tau}$
	LONG	FALSE ALARM $e^{-l/\tau}$	CORRECT REJECTION $1 - e^{-l/\tau}$

Fig. 1. Definition of hits, false alarms, correct rejections, and misses, and the mathematical expressions from which the probabilities of these events can be calculated according to Killeen and Fetterman (1988). See text for details.

which is the exponential decay function. Because Equation 3 is the probability of making a short response or judgment, it follows that

$$1 - (e^{-l/\tau}) \tag{4}$$

is the probability of a long response or judgment. For a two-stimulus discrimination with two choices, then, it is possible to predict the probabilities of hits, false alarms, correct rejections, and misses as illustrated in Figure 1 (the short stimulus is designated "s," and the long stimulus is designated "l").

The present experiment provides a test of Killeen and Fetterman's (1988) theory within a signal-detection context with rats. Rate of reinforcement was manipulated by varying the intertrial interval (ITI) on test days. Because the theory predicts that accuracy should decrease as the rate of reinforcement decreases, it was expected that the nonparametric signal-detection index of sensitivity,  $A'$  (Grier, 1971), would decrease with increasing ITI, and that the response bias index,  $B''$  (Grier, 1971), would indicate a decreased bias to report long with increasing ITI. Specific predictions from the theory were generated from estimates of hits and false alarms based on the equations in Figure 1.

METHOD

Subjects

Eight male albino Sprague-Dawley rats from the Walter Reed colony served as subjects. The animals were approximately 90 days old at the beginning of the experiment. The

rats were reduced to approximately 80% of their free-feeding body weights by restricted feeding. Water was available at all times in individual home cages.

Apparatus

The rats were trained in two standard operant-conditioning chambers, previously described by Raslear (1983, 1985). A PDP-11/73® computer controlled the experiment and recorded data. The experimental session for each subject occurred at approximately the same time each day, 5 days per week (excluding holidays). No water was available in the experimental chambers. The subjects were weighed after each session to determine the amount of supplemental food they would receive following the session.

Procedure

*Discrimination training.* A two-choice discrete-trials paradigm was used in which the animals were trained to discriminate between two durations of the houselight (0.1 and 10 s). Responses were effective only during the 5 s following the discriminative stimulus. A single correct response terminated the trial and produced a 45-mg Bio-Serv® food pellet, whereas a single incorrect response merely terminated the trial. If no response was made within 5 s, the trial terminated and no response to that stimulus was recorded. The intertrial interval was 5 s, during which time responses had no effect. Each stimulus occurred with a probability of .5 on each trial.

A session consisted of 320 trials, of which the first 20 were used as a warm-up for the animals. During discrimination training, performance on these trials was used to determine the conditions to which the animals would be exposed in the remaining 300 trials. If the animals produced a minimum of 90% correct responses during the warm-up, the remainder of the session consisted of noncorrection-procedure discrimination training. Otherwise, a correction procedure was in effect, in which the discriminative stimulus in whose presence the incorrect response was made was repeated 1 s following that response. The correction procedure was not in effect during the test phase.

*Testing.* The discriminative stimuli (0.1 and 10 s) remained the same as in the training phase. To produce a transient change in the

Table 1

Response totals, mean session time, and mean reinforcement rate for each rat as a function of the intertrial interval.

ITI (s)	Rat	Correct rejection: long response, long stimulus	False alarm: short response, long stimulus	Hit: short response, short stimulus	Miss: long response, short stimulus	Session time (s)	Rate of reinforcement (pellets per second)
1.0	111	267	24	306	3	2,364	0.122
1.0	112	295	4	300	2	2,426.5	0.122
1.0	211	296	0	304	0	2,185.5	0.137
1.0	212	288	2	310	1	2,267	0.131
1.0	311	295	4	302	1	2,134.5	0.139
1.0	312	288	5	308	1	2,848	0.106
1.0	411	285	10	305	0	2,267.5	0.130
1.0	412	329	1	269	1	2,394.5	0.125
2.5	111	281	11	306	2	3,444	0.085
2.5	112	299	1	299	1	2,741.5	0.109
2.5	211	305	2	292	1	2,672	0.112
2.5	212	299	1	299	1	2,658.5	0.113
2.5	311	307	2	291	0	2,671.5	0.112
2.5	312	282	4	312	2	3,143	0.095
2.5	411	326	3	267	4	2,819	0.105
2.5	412	297	0	303	0	2,628.5	0.114
5.0	111	299	3	295	3	5,026	0.059
5.0	112	299	4	272	3	4,852	0.065
5.0	211	287	1	311	1	3,313	0.090
5.0	212	284	1	315	0	3,364.5	0.089
5.0	311	326	0	273	1	3,491.5	0.086
5.0	312	282	2	316	0	3,820	0.078
5.0	411	297	1	300	2	3,481	0.086
5.0	412	315	0	285	0	3,528	0.085
10.0	111	299	6	281	7	5,857.5	0.050
10.0	112	317	1	274	8	5,396	0.055
10.0	211	312	1	276	11	5,161	0.057
10.0	212	304	4	258	34	5,039	0.056
10.0	311	309	2	262	27	5,072.5	0.056
10.0	312	271	4	319	6	5,462	0.054
10.0	411	288	1	307	4	5,060.5	0.059
10.0	412	297	0	299	4	5,058	0.059
20.0	111	215	6	152	46	6,299	0.029
20.0	112	211	0	218	13	6,299	0.030
20.0	211	212	1	148	71	6,299	0.029
20.0	212	236	0	131	72	6,299	0.029
20.0	311	227	7	190	24	6,299	0.033
20.0	312	217	3	193	23	6,299	0.033
20.0	411	221	4	200	15	6,299	0.033
20.0	412	213	4	215	18	6,299	0.034

reinforcement rate during the testing phase, an ITI of 1, 2.5, 5, 10, or 20 s was used on test days (Tuesdays and Fridays), and the 5-s ITI used in training was used on the remaining 3 baseline days. The ITI used on each test day was randomly determined for each rat. Each ITI was used on 2 test days, and the data from these 2 days were combined for each rat. Data from the baseline days were not used in the analyses of ITI effects.

## RESULTS

Table 1 presents total hits, false alarms, correct rejections, misses, mean session time and mean reinforcement rate for each rat as a function of the ITI. The data presented in Table 1 are the basis of all analyses to follow.

### *Reinforcement Rate*

Figure 2 shows the mean reinforcement rate as a function of the ITI. As expected, the ITI

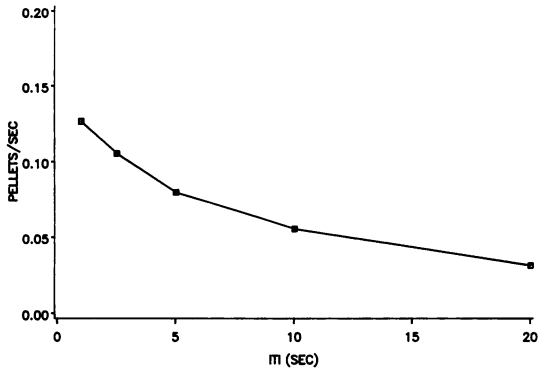


Fig. 2. Mean reinforcement rate as a function of the ITI averaged across all subjects.

was inversely related to the reinforcement rate (Friedman test,  $p < .01$ ; Bradley, 1968). Examination of Table 1 also indicates that the pattern observed in Figure 2 for the mean data is present in the data of each individual rat. Because Killeen and Fetterman's (1988) theory predicts that transient changes in reinforcement rate affect performance in timing tasks, this establishes that the ITI manipulation produced the minimal conditions necessary to test the theory.

### Sensitivity

In order to perform a signal-detection analysis of the data, *hits* were defined as short responses on trials in which the short stimulus (0.1 s) was presented, and *false alarms* (FAs) were defined as short responses on trials in which the long stimulus (10 s) was presented. The  $A'$  index of sensitivity (Grier, 1971), defined as

$$A' = \frac{\{(H - F) + (H - F)^2\}}{\{4H(1 - F)\}} + 0.5, \quad (5)$$

where  $H$  is the probability of a hit and  $F$  is the probability of an FA, was used because this measure is independent of specific assumptions concerning underlying distributions of sensory events (Egan, 1975; Green & Swets, 1966/1974).  $A'$  has a value of .5 when discriminative performance is at chance and a value of 1.0 when discriminative performance is perfect.

Predicted sensitivity was determined by setting the clock rate,  $\tau$ , proportional to the value of the ITI:

$$\tau = 0.24\{ITI + [(1 + s)/2]\}, \quad (6)$$

where  $l$  and  $s$  are the values of the long and

short discriminative stimuli. The values of  $\tau$ , in turn, were used in the equations of Figure 1 to generate values of  $H$  and  $F$  for use in predicting  $A'$  from Equation 5.

Figure 3 shows the  $A'$  values for the 8 rats as a function of the ITI. In general, sensitivity was highest at the 5-s ITI.  $A'$  declined slightly, or not at all, for shorter ITIs and declined dramatically at higher ITIs. Figure 4 shows the mean observed  $A'$  and the predicted  $A'$  value as a function of the ITI. There were statistically significant differences in sensitivity as a function of ITI (Friedman test,  $p < .01$ ) that mirror the predictions of Killeen and Fetterman's (1988) theory.

### Response Bias

Changes in response bias were indicated by the nonparametric signal-detection index (Grier, 1971),  $B''$ , defined as

$$B'' = \frac{[(H - H^2) - (F - F^2)]}{\div (H - H^2 + F - F^2)}. \quad (7)$$

$B''$  can have values between  $-1$  and  $+1$ . Given the definition of hits and FAs, negative values of  $B''$  indicate a bias to report short, whereas positive values of  $B''$  indicate a bias to report long. Killeen and Fetterman's (1988) theory predicts a decrease in bias to report long with increasing ITI. Therefore,  $B''$  should decrease (become more negative) with increasing ITI. Figure 5 shows the  $B''$  values for the 8 rats as a function of the ITI. Although there is considerable variability in  $B''$  at each ITI, it is clear that each animal demonstrated a trend for  $B''$  values to increase as the ITI increases. In general, the rats tended to report short for ITIs less than 5 s and to report long for ITIs greater than 5 s. Figure 6 shows the mean observed  $B''$  value and the predicted  $B''$  value as a function of ITI. For each animal, and for the group,  $B''$  became more positive with increasing ITI, a pattern that was statistically significant (Friedman test,  $p < .01$ ) and clearly counter to the predictions of the theory.

The ratio of long to short lever reinforcers was also calculated for each animal and ITI to determine if the change in response bias was reflected in the relative rate of reinforcement for the choice responses. For the group, this ratio was at a minimum of 0.98 at the 1-s ITI and at a maximum of 1.25 at the 20-s ITI. Although this pattern does follow the same trend as  $B''$ , it was not statistically significant

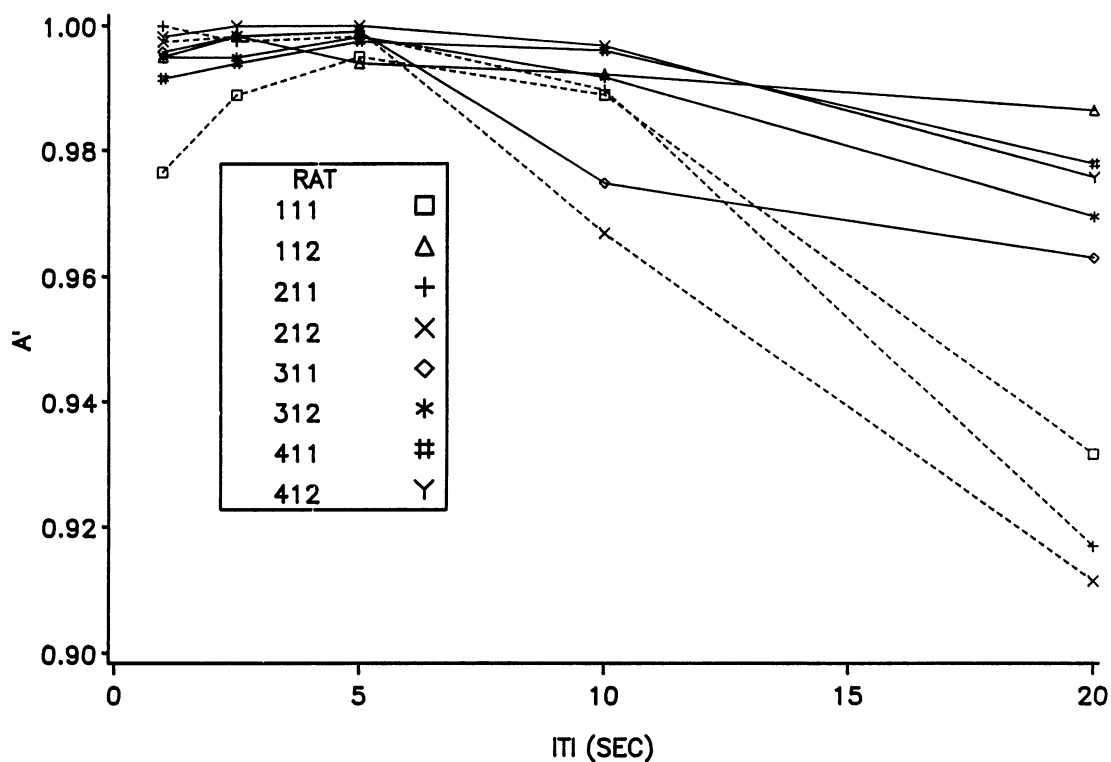


Fig. 3.  $A'$  values as a function of the ITI for individual subjects.

(Friedman test,  $p > .05$ ), which suggests that changes in response bias cannot be attributed to variations in the relative rate of reinforcement.

## DISCUSSION

Variations in ITIs on test days over a range of 1 to 20 s produced reliable changes in the rate of reinforcement in this experiment. According to Killeen and Fetterman (1988), the expected result of such transient changes in reinforcement rate is a decline in sensitivity and in the bias to report long as ITI increases. Sensitivity reliably declined with increasing ITI, but the bias to report long increased. This latter result is contrary to the predictions of Killeen and Fetterman's theory.

An alternative interpretation of Killeen and Fetterman's (1988) theory, however, exists. For instance, if  $n > 0$  in Equation 1 following the short (0.1-s) stimulus, then Equation 1 cannot be simplified to an exponential decay function. This, of course, implies that the rats pass through one or more behavioral states in 0.1

s. To model more than one behavioral state in the theory, one could use a cumulative normal distribution with mean and variance constrained by a Poisson assumption (Killeen & Fetterman, 1988, p. 283). Fortunately, such an analysis has been performed on the present data (P. R. Killeen, personal communication, December 15, 1989).

In this version of the model (P. R. Killeen, personal communication, December 15, 1989), the rate constant,  $\tau$ , is assumed to be a linear function of the reinforcement rate:

$$\tau = (C_1/T) + C_2, \quad (8)$$

where  $T$  is the reinforcement rate and  $C_1$  and  $C_2$  are constants. To maintain accuracy, the criterion ( $N$ ) for reporting long must shift as the rate of reinforcement changes:

$$N = C_3 T. \quad (9)$$

Given these assumptions, and a Poisson constraint, the mean ( $\mu$ ) and variance ( $\sigma^2$ ) are defined as

$$\mu = \sigma^2 = \tau(N + 1). \quad (10)$$

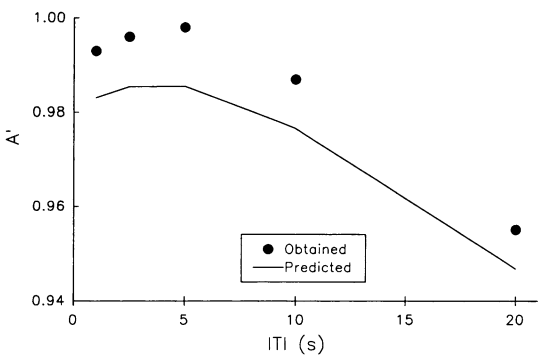


Fig. 4. Mean observed sensitivity and predicted sensitivity as a function of the ITI. The predictions are based on Killeen and Fetterman (1988).

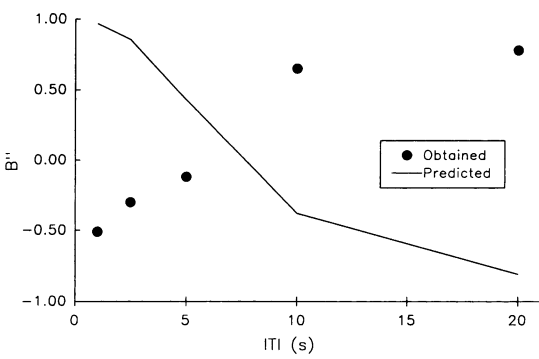


Fig. 6. Mean observed response bias and predicted response bias as a function of the ITI. The predictions are based on Killeen and Fetterman (1988).

The probability of a hit can then be defined as

$$p(\text{hit}) = 1 - \Phi[(s - \mu)/\sigma], \tag{11}$$

and the probability of a false alarm as

$$p(\text{FA}) = 1 - \Phi[(l - \mu)/\sigma], \tag{12}$$

where  $\Phi$  is the normal distribution function and  $s$  and  $l$  are the short and long stimuli. These values of  $p(\text{hit})$  and  $p(\text{FA})$  can then be

used in Equations 5 and 7 to generate predicted values for sensitivity and bias.

With the values of  $C_1$ ,  $C_2$ , and  $C_3$  set at 0.03, 0.9, and 33, respectively, the predictions of this model (P. R. Killeen, personal communication, December 15, 1989) are presented in Figure 7. Predicted sensitivity (top panel) does not change as rapidly as in the simple model (see Figure 4), but predicted bias (bottom

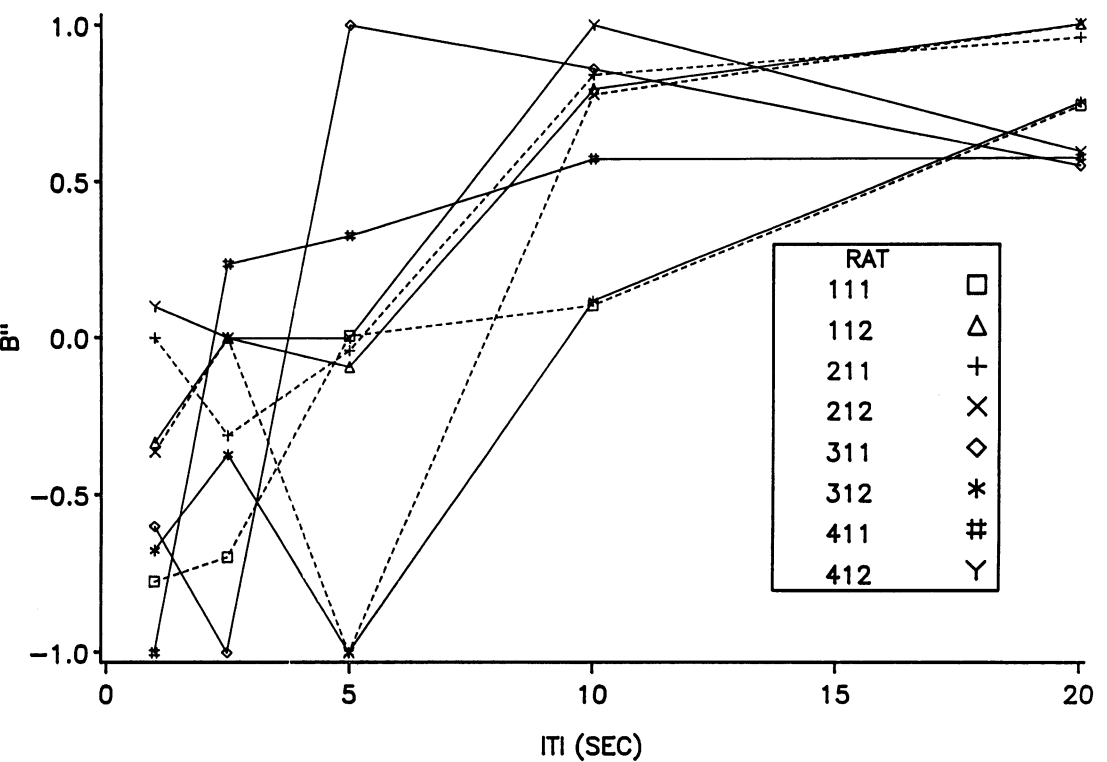


Fig. 5.  $B'$  values as a function of the ITI for individual subjects.

panel) is now substantially improved. On the whole, this version of Killeen and Fetterman's (1988) theory provides an adequate description of the data.

Scalar expectancy theory (SET) provides an alternative to the theory offered by Killeen and Fetterman (1988). According to SET (Gibbon, 1981; Meck, 1983) the probability of a hit is defined as

$$p(\text{hit}) = \Phi\{[(\sqrt{s})/\lambda s] - (1/\lambda)\}, \quad (13)$$

and the probability of a false alarm is defined as

$$p(\text{FA}) = \Phi\{[(\sqrt{s})/\lambda l] - (1/\lambda)\}, \quad (14)$$

where  $\lambda$  is the clock sensitivity. In the form of Equations 13 and 14, SET does not predict any effect of changing the ITI because the discriminative stimuli are not changing. However, if animals' behavior is controlled by the time between reinforcers (i.e., the nominal stimulus value plus the ITI) rather than the nominal discriminative stimuli,  $s$  and  $l$ , Equations 13 and 14 become

$$p(\text{hit}) = \Phi\{[(\sqrt{(s + \text{ITI})(l + \text{ITI})}) \div \lambda(s + \text{ITI})] - (1/\lambda)\} \quad (15)$$

and

$$p(\text{FA}) = \Phi\{[(\sqrt{(s + \text{ITI})(l + \text{ITI})}) \div \lambda(l + \text{ITI})] - (1/\lambda)\}. \quad (16)$$

As before, these values of  $p(\text{hit})$  and  $p(\text{FA})$  can be used in Equations 5 and 7 to generate predicted values for sensitivity and bias.

The top panel of Figure 8 presents the obtained and predicted values of  $A'$  for the SET model represented in Equations 10 and 11 with  $\lambda = 0.15$ . It is clear that SET does a good job of explaining the data if it is assumed that the animals' behavior is controlled by the time between reinforcers. The bottom panel of Figure 8 similarly presents obtained and predicted values of  $B''$ . The prediction here is considerably poorer than for  $A'$ , but the direction of the prediction is in the right direction.

The implication of the analysis above is that the nominal stimulus in a procedure that uses constant ITIs may not be the stimulus that controls behavior. This criticism, however, is not limited to such procedures. For instance, if the ITI was varied across trials, the mean ITI might still be incorporated into the duration that controls responding. Subject-initiated trials, which on the surface appear to eliminate the ITI, really only take control of the duration of the ITI from the experimenter

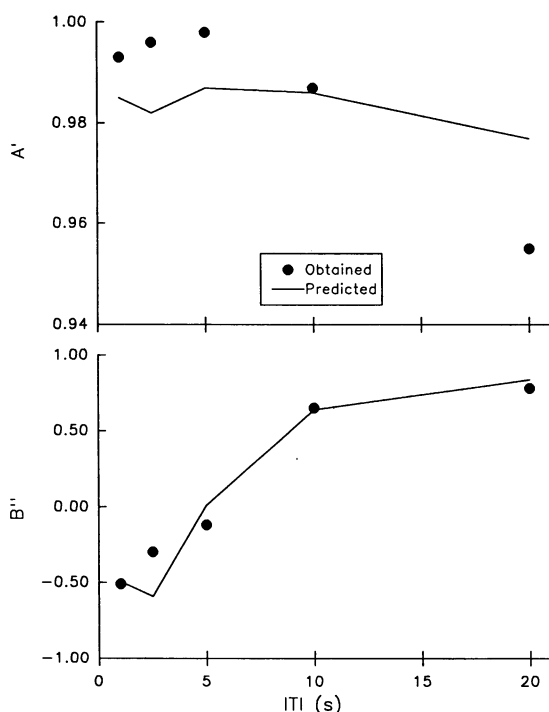


Fig. 7. A comparison of observed sensitivity (top panel), observed response bias (bottom panel), and the predictions made from a multiple-state model based on Killeen and Fetterman (1988). See text for details.

and place it with the subject. Time since the last reinforcer could still easily form the basis of accurate discriminations in such a procedure. A similar problem exists with regard to the effect of foreperiods on human reaction times (see Luce, 1986, pp. 71–81); thus, this situation is not unique to animal timing. Systematic investigation of the effects of fixed and varying ITIs (including subject-controlled ITIs) will be necessary to determine whether there is a methodological solution to this problem.

Although the definition of the stimulus in animal timing experiments is clearly an important issue for experimenters, the concern here is whether the application of SET in Equations 15 and 16 is reasonable. Apart from the poor performance of the model with regard to bias, other data suggest that this model is inadequate. For instance, Raslear (1983) reported time-bisection data in which a constant ITI (10 s) was used. The short stimulus was 0.1 s, and the long stimulus was 10 s. If the ITI was timed as part of the discriminative stimuli, the judged stimuli would be 10.1 and 20 s. SET predicts the geometric mean of the

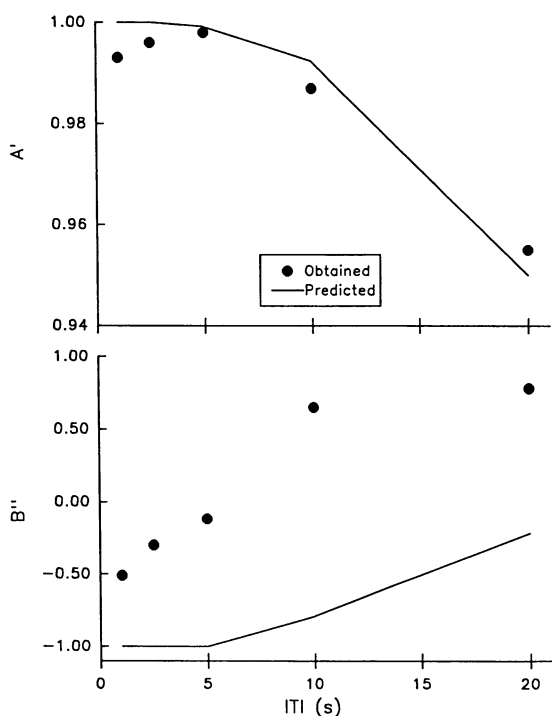


Fig. 8. A comparison of observed sensitivity (top panel), observed response bias (bottom panel), and the predictions made from scalar expectancy theory if interreinforcement time is judged. See text for details.

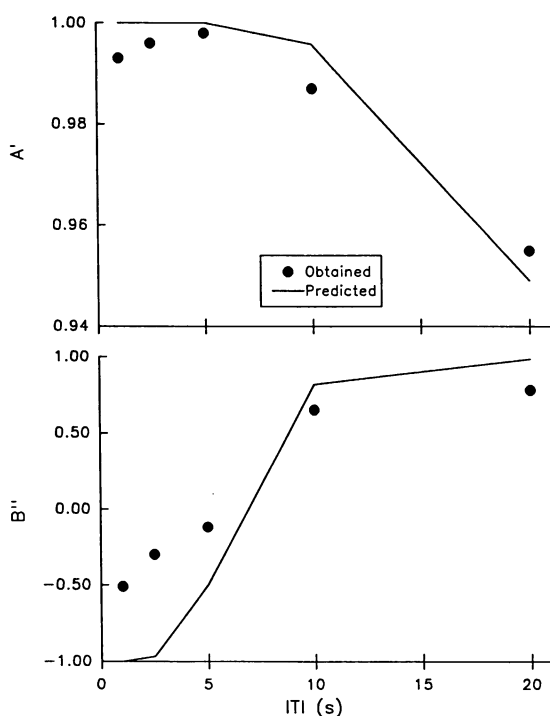


Fig. 9. A comparison of observed sensitivity (top panel), observed response bias (bottom panel), and the predictions made from scalar expectancy theory if switch variance is affected. See text for details.

short and long stimuli as the bisection point, which would then be 4.21 s (14.21 s minus the 10-s ITI). The mean bisection point obtained by Raslear was 1.39 s, which is higher than the predicted bisection point of the nominal stimuli [ $\sqrt{(0.1)(10.0)} = 1.0$ ] and considerably lower than the prediction for the nominal plus ITI durations. Thus, it seems unlikely that the application of SET, as described above, is a reasonable model.

Variations in the ITI in a discrimination task, however, are similar to variations in the foreperiod in reaction-time studies. In reaction-time studies, constant foreperiods (the situation most similar to that which exists in the present case) produce increases in the response latency as the duration of the foreperiod is increased (Luce, 1986). An explanation for this change in latency is that uncertainty concerning the stimulus onset increases with time and would, therefore, be proportional to the duration of the foreperiod. In SET, a mechanism called the "switch" (Gibbon & Church, 1984) could be similarly affected by changes

in the ITI. The switch opens and closes to allow an accumulation of pulses from an internal clock as the timed stimulus is turned on and off. The number of pulses accumulated is proportional to the duration of the stimulus and so allows the stimulus to be timed. The switch opens and closes with a latency, however, thereby introducing uncertainty (variance) concerning the exact duration of the stimulus. If changes in the ITI affect the latency of the switch opening in the same fashion as changes in the foreperiod affect the latency of a response in reaction-time experiments, then it is possible that uncertainty (variance) concerning stimulus durations also increases with increasing ITIs. To test this model, we assumed a linear relationship between uncertainty ( $\omega$ ) and ITI,

$$\omega = m\text{ITI} + b, \quad (17)$$

where  $m$  and  $b$  are constants. Gibbon and Church (1984) indicate that switch variance is independent of stimulus duration, so that



the probabilities of hits and FAs are

$$p(\text{hit}) = \Phi\{[(\sqrt{s})/((\lambda s) + \omega)] - (1/\lambda)\}, \quad (18)$$

$$p(\text{FA}) = \Phi\{[(\sqrt{s})/((\lambda l) + \omega)] - (1/\lambda)\}. \quad (19)$$

Predictions for this model, with  $m = 0.006$  and  $b = 0.09$ , are shown in Figure 9. At a qualitative level this model does quite well.  $A'$  decreases with increasing ITI, and  $B''$  reflects a change in bias from short to long. Considering that Equation 17 was arbitrarily chosen as a rule to estimate  $\omega$  from the ITIs and values of  $m$  and  $b$  have not been fit to minimize variance, the performance of this model is also adequate.

In conclusion, the data from this experiment suggest that, in its simplest form, Killeen and Fetterman's (1988) theory of animal timing is not adequate. Although Killeen and Fetterman make good predictions for sensitivity, predictions for bias were opposite to the observed changes in bias. A more complex version of the theory, however, makes adequate predictions for both sensitivity and bias. SET also makes adequate predictions for sensitivity and bias if it is assumed that the ITI affects variance in the switch function of that theory. Additional research on the effects of fixed and varying ITIs is required to guide further experimental and theoretical developments in this area.

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